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The evolutionary consequences of interspecific aggression

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Competition has always been a cornerstone of evolutionary biology, and aggression is the predominant form of direct competition in animals, but the evolutionary effects of aggression between species are curiously understudied. Only in the past few years, existing theoretical frameworks have been extended to include interspecific aggression, and significant empirical advances have been made. After arguing that agonistic character displacement (ACD) theory provides the most suitable theoretical framework, we review new empirical evidence for ACD and the results of mathematical models of the process. We consider how ACD can be distinguished empirically from ecological and reproductive character displacement and the additional challenges posed by developmental plasticity. We also provide the first taxonomically broad review of theoretical and empirical work on the effects of interspecific aggression on species coexistence and range limits. We conclude by highlighting promising directions for future research on the evolutionary effects of interspecific aggression.

Keywords: aggression; character displacement; coexistence; competitive exclusion; competitor recognition; interference competition; species recognition; reproductive interference

Introduction

Aggressive interference over access to resources is the predominant form of interference competition in animals. Aggression between species is very common and often just as intense and costly as intraspecific aggression.[1–3] Interspecific aggression must therefore have important ecological and evolutionary effects, but the study of interspecific aggression has lagged far behind that of other interspecific interactions, such as predation, parasitism, and mutualism. One symptom of this historical neglect is that there is no well-established theoretical framework or nomenclature for studying interspecific aggression. Indeed, most of what has been written on the subject is quite narrow in scope and only pertains to specific ecological contexts. The literature on interspecific aggression is a morass of overlapping terms with unclear meanings.[4–6] However, the meaning of

the term *aggression* itself is not controversial. It refers to physical attacks (e.g., pushing, biting, stabbing) and behavioral displays foreshadowing such attacks (e.g., territorial song, baring weapons, charging) that arise in the context of fighting over, for example, space, mates, food, or nesting sites. It does not include mechanically similar behaviors that arise in other contexts, such as predation, cannibalism, or forcible mating. Agonistic behavior is a broader term that encompasses aggression and other behaviors associated with fighting, such as submissive displays. Interspecific territoriality (defense of space) is the most common context in which agonistic interactions between species has been studied.[2,4]

Interaction between species typically begins upon secondary contact, when one or both species expands into the other's range. The initial behavioral response to heterospecifics is unlikely to be adaptive, simply because the species were previously evolving in isolation from each other. Species that do not

initially respond aggressively to each other may nevertheless be in competition for limiting resources, and if the species coexist long enough in sympatry, adaptive interspecific aggression could evolve *de novo*.[7–9] Alternatively, interspecific aggression could arise as a byproduct of intraspecific competition, particularly among species that use similar agonistic cues and recognition mechanisms by virtue of common ancestry,[10–14] whether or not they have limiting resources in common. The degree of resource overlap between species, and other factors such as the cost of fighting, will likely determine whether selection favors increases or decreases in interspecific aggression relative to the initial level.[4] Aggression between species could also arise as a byproduct of intraspecific competition in cases of primary contact, that is, when speciation occurred in parapatry or sympatry, with no allopatric phase. In general, selection in sympatry is likely to modify traits that affect the rate or intensity of aggressive interactions,[4] and may cause sympatric populations to diverge from allopatric populations.[15]

While the evolutionary consequences of cross-species mating have been studied extensively, both empirically and through mathematical models,[16–24] the evolutionary consequences of aggression between species have been relatively unstudied.[1,2,4,6] The predicted effects of interspecific aggression are diverse and include competitive exclusion and range shifts,[25–31] and various forms of character evolution, including shifts in traits that affect interspecific encounter rates (e.g., habitat preferences, activity schedules), fighting ability (e.g., weaponry, body size), and competitor recognition (e.g., coloration, song, response thresholds to agonistic cues).[4,7,8,15,32–38]

The goal of this review is to help promote the study of interspecific aggression forward and into the mainstream of evolutionary biology. We start by reviewing recent efforts to incorporate interspecific aggression into existing theoretical frameworks. We argue that character displacement theory offers a better framework for interspecific aggression than does optimality theory. After reviewing classical character displacement theory, we discuss two alternative approaches that have been proposed for incorporating interspecific aggression into this framework: (1) leaving the established definitions of character displacement intact and recognizing a third character displacement process caused by interspecific aggression,[4] or (2) expanding the definitions of reproductive character displacement (RCD) and ecological character displacement (ECD) to include the effects of interspecific aggression.[32] We conclude that the first approach is preferable, and we refer to the third character displacement process as agonistic character displacement (ACD).[4] We then highlight recent case studies that provide new evidence for ACD and that illustrate a range of possible outcomes. Next, we discuss the importance of mathematical models for studying character displacement processes and review progress to date in modeling ACD. We then take up the question of how ACD can be distinguished empirically from ECD and RCD and identify priorities for future data collection. The theoretical and empirical challenges posed by developmentally plastic responses to heterospecifics are also discussed briefly. We then turn to two closely related questions at the interface of ecology and evolution: does interspecific aggression impede or promote coexistence between species, and to what extent are competing species' range limits set by interspecific aggression? In the final section, we reiterate our main conclusions.

Optimal aggression theory

Several researchers have approached interspecific aggression as an optimality problem.[2,39,40] Mikami and Kawata[39] developed an optimal interspecific territoriality model based on Charnov's[41] multispecies optimal prey choice model. Territory holders were assumed to have perfect information and complete control over access to their territories and were predicted to exclude heterospecifics whenever it is profitable to do so. To our knowledge, Mikami and Kawata's[39] specific predictions have not been tested empirically. Peiman and Robinson[2] assumed that interspecific aggression is usually adaptive and made several predictions about how the level of aggression toward heterospecifics ought to vary as a function of factors such as resource overlap, resource abundance, and population density. They found some support for their predictions in a meta-analysis of empirical studies but cautioned that evolutionary history also needs to be considered. Ord *et al.*[40] assumed that interspecific aggression is usually not adaptive and adapted Reeve's[42] optimal kin recognition model to make predictions about the evolution of species recognition under different scenarios. Given the trait distributions of

conspecific and heterospecific cues, the encounter rate with heterospecifics, the cost of incorrect responses, and the benefit of correct responses, their model predicts the optimal response thresholds in mating and territorial encounters. In a meta-analysis of species recognition studies, Ord *et al.*[40] found scant support for their model's general predictions and concluded that the benefits and costs of responding to heterospecifics are probably species specific.

A well-known problem with applying optimality theory to behavioral interactions is that the optimal behavior is likely to depend on how other individuals behave.[43] This problem is only compounded when the potential interactors include members of other species. Optimality theory also fails to account for evolutionary time lag and gene flow. Species that have recently come into secondary contact, or that are in contact in only a small part of their ranges, may not be locally adapted in the zone of sympatry. We think interspecific aggression should be conceptualized and modeled as an interaction between two (or more) evolving populations. As such, character displacement theory offers a better starting point than optimality theory.

Character displacement theory

Brown and Wilson[44] defined character displacement as a geographic pattern in which, "when two species of animals overlap geographically, the differences between them are accentuated in the zone of sympatry and weakened or lost entirely in the parts of their ranges outside this zone." They proposed that this pattern likely results from two specific processes, acting individually or in concert: selection against cross-species mating, which they termed reinforcement, and selection against interspecific exploitative competition, which they termed ecological displacement. The first process is now commonly referred to as reproductive character displacement (RCD), while the second process is referred to as ecological character displacement (ECD).[45] Some authors still use the term *reinforcement* in the way that Brown and Wilson[44] did, synonymous with RCD, but other authors restrict this term to cases in which nonsterile hybrid offspring are produced.[17,46] Confusingly, the terms RCD and ECD are also commonly used to refer to the geographic patterns that Brown and Wilson[44] described, whether or not those patterns were caused by selection against cross-

species mating or exploitative competition. Character displacement processes can produce a variety of geographic patterns, including both convergence and divergence in sympatry, or no geographic pattern at all.[45,47,48] For some research questions, the geographic patterns may be of greater interest than the processes that produced them,[49] but here we are primarily interested in the evolutionary processes that result from interspecific interactions.

Brown and Wilson[44] were quite emphatic that ecological displacement is caused by indirect (exploitative) competition, not by direct (interference) competition. They suggested that aggression between competing species might evolve as an alternative to ecological displacement, but they did not consider the possibility that selection against interspecific aggression might accentuate species differences. Lorenz[36,50] assumed that interspecific aggression would usually be selected against and proposed that species differences in agonistic cues (e.g., coloration, song, scent marks) evolve in part because they enable territorial animals to recognize competitors of their own species while avoiding unnecessary and costly interactions with noncompetitors. Cody[7,51] focused on cases of secondary contact between ecological competitors and hypothesized that selection in sympatry favors convergence (or prevents divergence) in agonistic cues. The advantage of resembling competitors of another species, Cody argued, is that this facilitates interspecific territoriality and spatial partitioning of resources. Gill[9] coined the term α-*selection* to refer to selection favoring increases in interspecific competitive ability through interference mechanisms, including aggression. For decades, these ideas about interspecific aggression remained virtually unconnected in the literature.

Grether *et al.*[4] extended character displacement theory to include the evolutionary effects of interspecific aggression by introducing the concept of agonistic character displacement (ACD). ACD can be defined as the process of phenotypic evolution caused by interference competition between sympatric species. The term *interference competition* is used broadly here to include any harmful interaction between individuals over access to a resource, whether or not the resource is in limited supply.[52,53] By this definition, interspecific territoriality (defense of space) qualifies as interference competition, regardless of whether the species actually

overlap in resource use. The evolutionary effects of ACD may include improvements in interspecific fighting ability, temporal or spatial shifts in activity, improvements in competitor recognition, and shifts in agonistic cues, or a combination of these.[4]

Grether *et al.*[4] modeled the evolution of agonistic cues and competitor recognition and showed that varying the intensity of interspecific exploitative competition relative to intraspecific exploitative competition (E) was sufficient to switch the evolutionary dynamics from divergence at low E (Lorenz's scenario[36,50]) to convergence at high E (Cody's scenario[7,51]). Thus, unlike RCD, ACD does not necessarily cause sympatric species to diverge phenotypically. Unlike ECD, ACD does not necessarily reduce the overall level of competition between species. In a critical review of the literature, Grether *et al.*[4] found 33 putative examples of ACD across diverse animal groups (15 divergence examples; 18 convergence examples; see the Case Studies section for additional examples). Note that character convergence has long been considered to be a possible outcome of character displacement processes; displacement is a neutral term with respect to the direction of the shift. Quoting Grant,[47] "since the mechanism is the same in both cases, natural selection arising from the presence of another similar species, it seems logical to use the term *displacement* for both, but to contrast the direction and result of the displacement by the terms convergent and divergent."

The alternative to defining a new character displacement process is to expand the definitions of RCD and ECD to include the effects of interspecific aggression. RCD has long been considered to include the evolutionary effects of reproductive interference between species before mating.[54] Previously, reproductive interference was taken to mean male–female interactions between species, such as attraction to heterospecific courtship song, but Gröning and Hochkirch[18] expanded the concept to include intrasexual aggression between species over access to mates (heterospecific rivalry). Whether this was Gröning and Hochkirch's intention is not clear to us, but other authors have suggested that heterospecific rivalry can cause RCD.[15] Besides lumping together the potentially disparate effects of intrasexual and intersexual interactions between species, this scheme leaves out aggression between species that is not clearly related to mate competition, and as Gröning and Hochkirch[18] acknowledged, in many cases aggression is not purely sexual or nonsexual (e.g., competition over all-purpose territories).

Pfennig and Pfennig[32] expanded the definitions of both ECD and RCD to include the effects of interspecific aggression. Their criterion for whether interspecific aggression causes ECD or RCD is whether the aggression is based on competition for reproductive opportunities (RCD) or not (ECD), but they do not explain how this distinction should be made in practice. For example, in the case of species that defend year-round interspecific territories, should interspecific aggression be classified as reproductive during the breeding season and nonreproductive outside the breeding season, or, instead, should aggression during the breeding season be partitioned into reproductive and nonreproductive components? Pfennig and Pfennig's[32] scheme results in a model in which ECD can be caused either by indirect competition (e.g., depletion of a common limiting resource) or by direct competition (i.e., aggression). This is a major departure from the way that ECD has been conceptualized for over 50 years. All formal, mathematical models of ECD have focused on competition caused by resource depletion, and the evolvable traits in such models (if explicit) are framed as traits affecting resource use.[48,55–59] Pfennig and Pfennig[32,45,46,60] maintain that character displacement always reduces the overall level of competition (for mates or other resources) between species, and they offer this as the unifying theme for their synthesis, but this model fails to incorporate cases of adaptive aggression between ecological competitors. Enhancements in competitor recognition or interspecific fighting ability may favor one species over the other, but they do not necessarily reduce the overall strength (i.e., cost) of the interaction.

To summarize, redefining RCD and ECD to include the evolutionary effects of interspecific aggression generates a conceptual discontinuity in the character displacement literature and requires the incorporation of distinctly different evolutionary processes. If the goal is to develop process-based, as opposed to pattern- or context-based, definitions of character displacement, the solution proposed by Grether *et al.*[4] accomplishes this without modifying the long-established concepts of RCD and ECD. For clarification of the relationships among
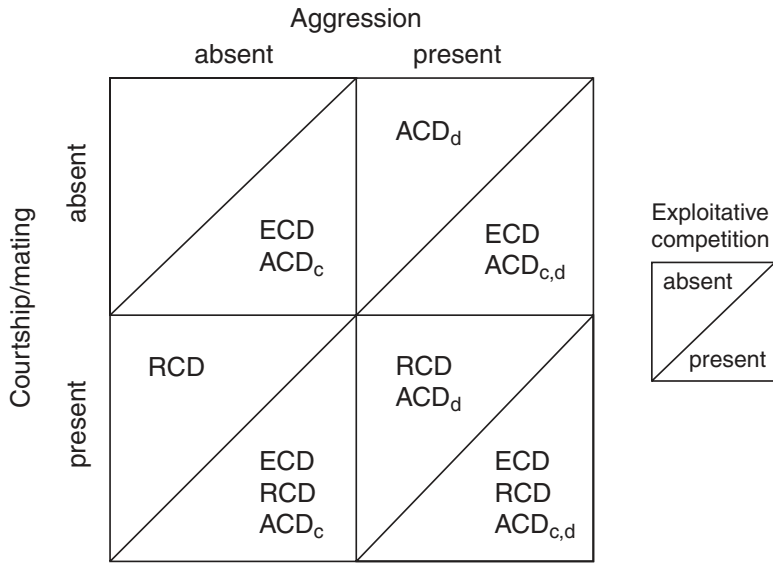
Figure 1. Character displacement processes possible, given the presence or absence, at the time of secondary contact, of three different types of interspecific interactions: exploitative competition (i.e., depletion of a common limiting resource), courtship or mating, and aggression. Within each square, exploitative competition is absent above and present below the diagonal. ACD can be either convergent (ACD_c) or divergent (ACD_d), and in some cases, either outcome is possible. When species compete exploitatively, but do not initially respond aggressively to each other, interspecific aggression may evolve *de novo*, which is considered to involve convergence in competitor recognition systems (ACD_c). When species compete exploitatively and also respond aggressively to each other at the time of secondary contact, equal competitors might converge in competitor recognition (ACD_c), but if one species is superior at interference competition, the subordinate species might diverge in ways that reduce interspecific aggression (ACD_d).

ACD, RCD, and ECD, and the basic conditions under which each process might occur, see Figure 1.

An important consequence of distinguishing ACD from ECD is that it requires investigators seeking to link theory to data to be more precise about the fitness consequences and evolutionary implications of different processes underlying interspecific competition. Models of character displacement based on Lotka–Volterra competition equations,[58,61,62] describe the fitness costs of competition as a phenomenological per-capita effect that can be interpreted to subsume the fitness costs of both resource-mediated competition and aggression. However, partitioning competition into its composite elements is fundamental to distinguishing the effects of exploitative competition from those of interference competition. Likewise, distinguishing between (1) selection on females to recognize the species identity of prospective mates (i.e., RCD) and (2) selection on males to avoid competing for mates with males of other species (i.e., ACD) allows investigators to compare and contrast the evolutionary consequences of these distinct

mechanisms.[151] Recognizing ACD, ECD, and RCD as distinct evolutionary processes does not require the assumption that they always operate independently of each other.[15] On the contrary, recognizing the distinctions between these processes is a prerequisite to studying how they interact (see Formal Theory).

Case studies

This section highlights three recent studies that contribute to the growing literature on the evolutionary effects of interspecific aggression. These examples illustrate that aggressive interactions between species can lead to various outcomes. For a critical review of other possible examples of ACD and a list of empirical criteria, see Ref. 4.

Rubyspot damselflies
In many species, the primary or sole function of male territoriality is to obtain priority of access to conspecific females.[63–65] Logically, males should only defend mating territories against conspecific males, but closely related species often have similar
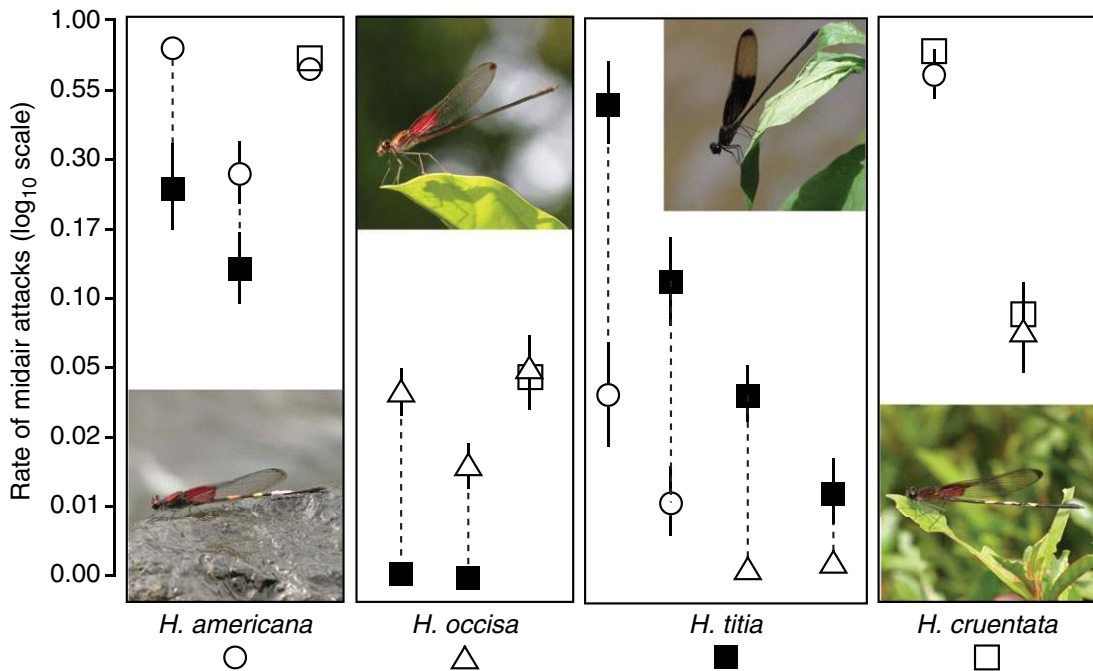
Figure 2. Aggressive responses of territory holders of four species of *Hetaerina* damselflies (named below graphs and shown in photos) to tethered male conspecific and sympatric congener intruders. Symbols identify the species of the intruders (see the key below the graph). Vertical dashed lines connect means (± SE) for tests carried out at the same site. Overlapping points are not significantly different; all others $P < 0.05$. Note lack of discrimination between species that are similar in coloration. Redrawn using data published by Anderson and Grether.[75]

competitor recognition systems. When such species come into secondary contact, selection would be expected to drive divergence in ways that reduce interspecific aggression (i.e., divergent ACD).

All species of rubyspot damselflies (*Hetaerina* spp.) have red wing pigmentation, but species vary in the number, size, shape, and position of red spots and in the amount of black wing pigmentation. Wing coloration affects a male's ability to hold a mating territory, and consequently, his mating success.[66,67] Rubyspot territories are analogous to the display courts of classic lekking species, except that males do not perform courtship displays. While the territories are located in areas where females prefer to lay eggs, males do not control access to oviposition material and females rarely oviposit in their mate's territory.[66,68–71] Both sexes feed at times when or places where males are not territorial.[72] Thus, besides females, there are no resources over which territorial males compete. Since territorial males compete only for access to potential mates, fighting with heterospecific males would not seem adap-

tive. Nevertheless, interspecific territoriality does occur.[73,74]

Territorial responses to heterospecific males are influenced by the degree of phenotypic similarity between sympatric species.[75] Territory holders in sympatric species pairs with similar coloration do not discriminate between conspecific and heterospecific intruders, while those in sympatric species pairs with dissimilar coloration show reduced aggression toward heterospecific intruders (Fig. 2). Phenotypic manipulations confirmed that wing coloration affects responses to territory intruders.[75] Adding black coloration to intruders' wings increased aggression from *H. titia,* a species with prominent black wing spots. The same manipulation reduced territorial responses from *H. americana* and *H. occisa,* two species without black wing spots, but only at sites where *H. titia* also occurs (Fig. 3). At allopatric sites, *H. americana* and *H. occisa* showed no difference in aggression toward blackened and control intruders (Fig. 3). Wing coloration also shows a character displacement
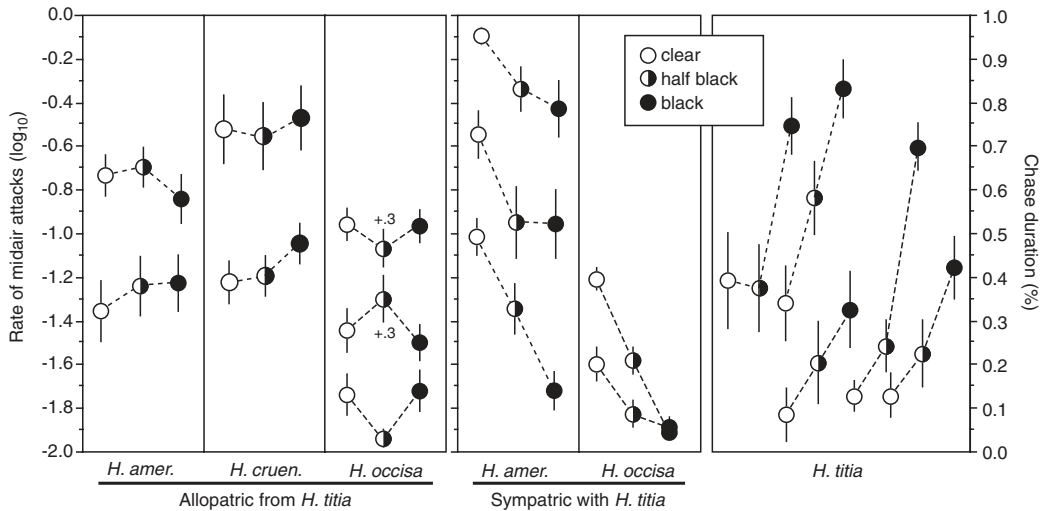
Figure 3. Evidence for character displacement of competitor recognition in rubyspot damselflies. Summary of results from multiple sites where territory holders were presented with tethered *Hetaerina americana* or *H. occisa* intruders (dashed lines connect means ± SE for the same site). Tethered males were given one of three wing color treatments: clear, half black/half clear, or black. Adding black to the wings increases the resemblance to *H. titia* (see Fig. 2). The graphs show that blackening the wings of tethered *H. occisa* or *H. americana* intruders resulted in increased aggression from *H. titia* territory holders (right panel), reduced aggression from *H. occisa* and *H. americana* territory holders in sympatry with *H. titia* (middle panel), and had no significant effect on aggression from *H. occisa*, *H. americana*, or *H. cruentata* in allopatry (left panel). The effect of sympatry with *H. titia*, as measured by the treatment by site category interaction, was highly significant for both *H. occisa* and *H. americana* ($P < 0.001$). For clarity, points for two *H. occisa* populations are displaced vertically by the number of $\log_{10}$ units indicated. Redrawn using data published by Anderson and Grether.[75]

pattern.[76] Within the zone of sympatry, the relative abundance of heterospecifics influences the extent of the black coloration in *H. titia*. Where *H. occisa* or *H. americana* are numerically dominant, black spots in *H. titia* tend to be larger than at sites where *H. titia* is numerically dominant.

These sympatric shifts in wing coloration and competitor recognition, both of which reduce interspecific fighting,[74] provide strong evidence for divergent ACD. However, a mathematical model based on this system shows that RCD would likely dominate ACD if females used wing coloration for mate recognition (see Formal Theory). Heterospecific mating attempts do occur, but even if there was no ongoing selection against cross-species mating, RCD could have occurred in the evolutionary past. The critical question is whether female *Hetaerina* use male wing coloration for mate recognition, and while no evidence has been found that they do, the possibility has not been ruled out.

Antbirds

Interspecific territoriality may be adaptive for species that defend all-purpose territories.[77] Selec-

tion in sympatry may favor increased aggression toward heterospecific rivals[6,9,78,79] and convergence in agonistic cues.[4,5,7,51]

Antbirds (Thamnophilidae) are a diverse family of mostly Neotropical passerines. Many species defend year-round, all-purpose territories, and both sexes often sing highly stereotyped territorial songs, with no evidence for song learning.[80,81] Across the family, territorial songs are more divergent between sympatric species than allopatric species.[82]

Two Amazonian nonsister taxa, however—*Hypocnemis peruviana* and *H. subflava*—have strikingly similar territorial songs despite broadly overlapping distributions. One well-supported hypothesis for this similarity is that song convergence aids in competitor recognition, facilitating interspecific territoriality.[5] Male and female songs within each species are quite distinct, but within each sex, the songs of two species are barely distinguishable. This overlap in territorial song is particularly striking because the two species clearly differ in plumage color and nonterritorial vocal signals (Fig. 4). The species have converged in competitor recognition as well: allopatric male *H. peruviana* has weaker
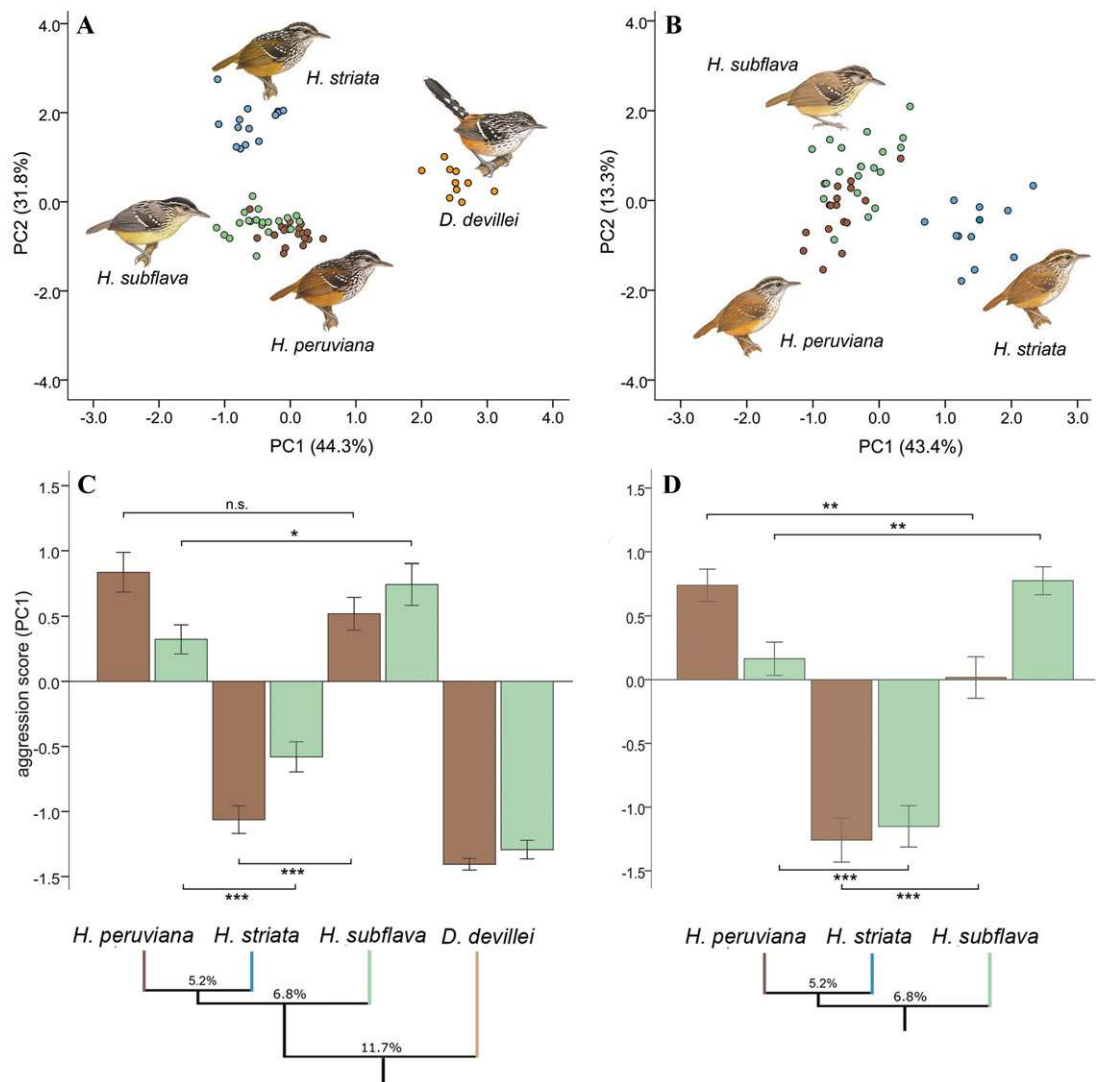
Figure 4. Evidence for convergent agonistic character displacement in the territorial songs of the antbirds *Hypocnemis peruviana* and *H. subflava*.[5] Despite conspicuous interspecific differences in plumage color, the sympatric *H. peruviana* (brown circles) and *H. subflava* (green circles) overlap in male (A) and female (B) territorial song characteristics. Responses of sympatric male (C) and female (D) *H. peruviana* (brown bars) and *H. subflava* (green bars) to song playback show a clear pattern: both sexes responded more aggressively toward conspecific song and the song of their sympatric congeners than to the songs of an allopatric congener *H. striata* (despite, in the case of *H. peruviana*, that *H. striata* is actually a closer relative than is *H. subflava*). A simplified phylogeny of the antbird species whose territorial songs were used as playback is reproduced as part of the horizontal axis labels of C and D. Reproduced with permission from the authors and John Wiley & Sons.

responses to heterospecific than conspecific song, but sympatric males are equally aggressive to playback of songs from either species (Fig. 4). Convergence through adaptation to a common acoustic environment seems unlikely in these species; on average, they have quite different habitat preferences in sympatry.[83] Additional work has demonstrated

convergence in song while controlling for environmental gradients (J.A. Tobias, N. Seddon, A.N.G. Kirschel, unpublished data). The species have not been observed to hybridize; playback experiments on captive birds have demonstrated that females of both species can reliably distinguish conspecific from heterospecific male territorial songs.[83] This

suggests that convergence in male territorial songs does not cause confusion over species identity in a mating context (otherwise, song convergence would presumably have been blocked by RCD).

Anoline lizards

In some secondary contact zones, interspecific aggression may be adaptive for one species and maladaptive for the other. In anoles (Polychrotidae), interspecific competitive interactions may drive rapid (< 40 years) shifts in both morphology and behavior, but species differences in interference competitive ability or population density may cause such shifts to be asymmetric. Most species are generalist insectivores, and many defend all-purpose territories. Anole species are classified into ecomorphs with shared morphological, ecological, and behavioral characteristics;[84,85] in natural communities, anoles of the same ecomorph are seldom broadly sympatric. Communities assembled through human-mediated biological invasions, however, do not always follow this pattern.

Two invasive trunk-ground anoles, the Cuban *Anolis sagrei* and the Puerto Rican *A. cristatellus*, have become broadly sympatric in Miami since the mid-1970s.[86–89] These two species differ in size (*A. cristatellus* average approximately two times the mass of *A. sagrei*) and perhaps in fighting ability; staged contests in experimental arenas tend to favor the larger *A. cristatellus*.[90] Sympatric male *A. sagrei* are less aggressive toward *A. cristatellus* than are allopatric males (Fig. 5), suggesting that agonistic interactions with much larger heterospecific rivals are not adaptive. No such effect was observed in *A. cristatellus*, which were aggressive toward *A. sagrei* in both sympatry (Florida) and allopatry (Puerto Rico). While *A. cristatellus* may be behaviorally dominant, *A. sagrei*—which invaded Florida much earlier than *A. cristatellus*—would have been numerically dominant early in the invasion of *A. cristatellus*, and competition with *A. sagrei* may have influenced the evolution of *A. cristatellus*. Sympatric male *A. cristatellus* have more robust heads and greater bite force than do allopatric males, a shift that makes sympatric *A. cristatellus* more divergent from *A. sagrei* than allopatric *A. cristatellus* (Fig. 5). Bite force affects both prey processing and fighting ability, so this sympatric shift in bite-related morphology may result from exploitative competition, interference competition, or both.[90]

Formal theory

ACD theory seeks to examine whether selection arising from interspecific aggression can generate observed geographic patterns of phenotypic variation. Formal theory might not be necessary if the verbal predictions were simple or if it were easy to elucidate the causative mechanisms underlying observed patterns through empirical work. But the predictions of ACD theory are not simple and identifying the evolutionary mechanisms underlying geographic patterns of trait variation is a major challenge (see below). Multigenerational manipulative experiments can yield important insights about evolutionary processes, but they require extremely tractable model organisms and extrapolating the results to other species can be problematic.[91] Dynamic mathematical models provide a promising approach for systematically analyzing how different processes might interact to generate particular patterns of trait variation.[92] They can help clarify which outcomes are most likely, or even possible, based on a given set of assumptions.[93] Models can also provide a framework for integrating and interpreting data from diverse spatial and temporal scales.[94]

Formal theory for ACD has focused primarily on the evolution of traits affecting competitor recognition, mainly because most of the likely cases of ACD documented in the literature involve shifts in such traits.[4] Modeling competitor recognition requires the clarification of assumptions concerning several key processes that are best formulated at the individual level. For example, to characterize what happens when populations of two potentially interacting species come into contact, accounting for how heritable phenotypic variation (the raw material of character displacement) affects the fitness consequences of encounters between individuals is key.[95] As formulated by Grether *et al.*,[4] encounters between individuals can result in mutual recognition, one-sided recognition, or mutual nonrecognition, depending on the phenotypes of the two individuals; the fitness consequences of encounters further depend on whether they are between conspecifics or heterospecifics. This model predicts that when exploitative competition between two sympatric species is strong relative to intraspecific competition, and aggression affects access to the common resources, the competitor recognition systems of the two species should converge and
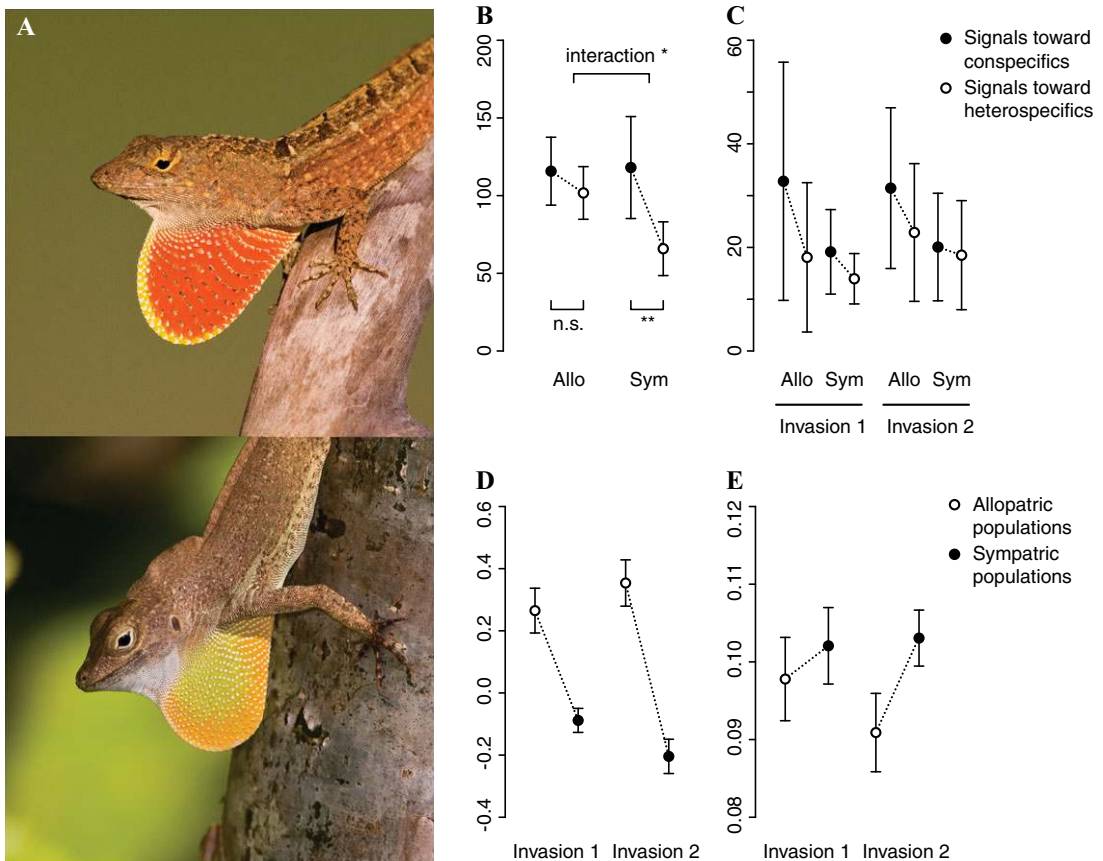
Figure 5. Sympatric shifts in behavior and morphology in *Anolis* lizards.[90] (A) Top: male *A. sagrei*; bottom: male *A. cristatellus.* (B) Number of signaling behaviors (pushups, head-bobs, and dewlap displays) by male *A. sagrei* during staged territorial intrusions by conspecific and heterospecific rivals. (C) Number of signaling behaviors by male *A. cristatellus* during staged territorial intrusions. (D) Sympatric *A. cristatellus* have a lower head shape score, representing a sympatric shift toward shorter, broader, and deeper heads ($P < 0.001$; interaction with invasion not significant). (E) Sympatric *A. cristatellus* bite harder than allopatric males, after controlling for snout-vent length (SVL) ($P = 0.036$; interaction with invasion not significant); maximum bite force (N) divided by SVL (mm) is shown. Invasions 1 and 2 are two independent invasions of *A. cristatellus* into Florida from different Puerto Rican source populations. Invasion 1 includes allopatric males in Fajardo, PR, and sympatric males in South Miami, FL. Invasion 2 includes allopatric males in San Juan, PR, and sympatric males on Key Biscayne, FL. Means and 95% confidence intervals are shown in each plot. Key to significance symbols: *n.s.* not significant; * $P < 0.05$; ** $P < 0.01$. Data from Ref. 90 and photos by N. Losin.

interspecific aggression should increase (Fig. 6). Conversely, when interspecific exploitative competition is weak relative to intraspecific competition, the competitor recognition systems should diverge and interspecific aggression should decrease (Fig. 6). Furthermore, the level of interspecific exploitative competition at which the dynamics switch from divergence to convergence depends on the costs of fighting.[4] The influences of other factors, such as differences between species in competitive dominance, remain to be studied. Such factors are likely to be common in real competitive systems,[96] and

formal theory provides a crucial tool for elucidating how they can influence the effects of interspecific aggression on the direction of character shifts.

Indeed, dynamic models provide a means to compare the relative efficacy of different evolutionary processes and to theoretically examine how they interact. Such models may help guide the direction of future empirical research. For example, Okamoto and Grether constructed a dynamic model based on territorial damselflies that investigated how ACD and RCD would interact if the same male trait
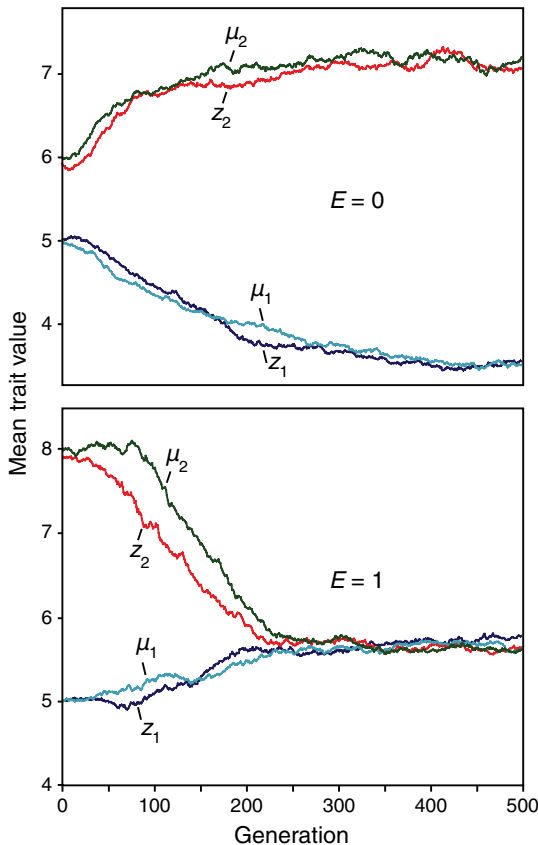
Figure 6. Sample ACD model simulation runs. The competitor recognition system modeled consists of a recognition cue z and a Gaussian response function defined by location parameter μ and width parameter σ. The probability that a resident of a territory will respond aggressively to an intruder peaks when the intruder's value of z equals the resident's value of μ, and vice versa. The simulations explore the effects of secondary contact between species with similar competitor recognition systems and in which both z and μ are genetically heritable. If the two species are not ecological competitors ($E = 0$) but are initially aggressive toward each other, z and μ can diverge rapidly between species until interspecific aggression is largely eliminated (upper panel). If, instead, the species are strong ecological competitors ($E = 1$) but do not initially treat each other as such, z and μ can converge between species until they treat each other as competitors and engage in aggressive interactions (lower panel). The subscripts on z and μ identify the species (e.g., z_1 is the mean phenotypic trait value for species 1). Reproduced from Grether *et al.*,[4] with permission from John Wiley & Sons Inc.

(e.g., wing coloration) were used both for male competitor recognition and female mate recognition (males are assumed to mate indiscriminately.[151] Although the model was parameterized for damselflies, the results are expected to apply to other taxa

in which males compete for mating territories. The model predicted that divergence in male competitor recognition, as well as in the trait upon which recognition is based, would be driven by RCD rather than by ACD, regardless of the relative strengths of selection against interspecific aggression and interspecific mating (Fig. 7; Okamoto and Grether[151]). The dominance of RCD over the evolutionary trajectory stems from the need for males to be recognized by conspecific females. From an empirical standpoint, these results are alarming because it means that RCD, driven by selection on females to select conspecific mates, could produce patterns of character divergence fully consistent with the predictions of ACD.

Distinguishing between processes empirically

The ideal approach to the study of character displacement is to examine evolution in action from the time of secondary contact, but this requires exceptional timing and long-term funding. Perhaps the only example is the Grants' more than 30 year study of Darwin's finches (*Geospiza* spp.), which provided unparalleled evidence for ECD.[97] The most common approach is to document a geographic pattern consistent with character displacement (e.g., divergence in sympatry) and then garner additional data to narrow down the list of possible processes that could have produced the pattern.[98] An alternative approach is to study taxa in which a particular character displacement process likely occurred and test for the predicted geographic patterns.[76,90] Starting with evidence for a species interaction (e.g., interspecific aggression) may be more promising, from the standpoint of studying the evolutionary consequences of that particular interaction, than starting with a pattern. On the other hand, character displacement processes need not leave a detectable geographic pattern. Character shifts that evolved in sympatry may spread into allopatry or become obscured by environmental gradients, or the species may have become sympatric throughout most of their ranges.[48] Regardless of the initial approach, the same types of data ultimately are needed to build a compelling case for character displacement. For a full list of criteria for establishing whether a geographic pattern is likely to have been caused by ACD, see Ref. 4. Here we focus more narrowly, and
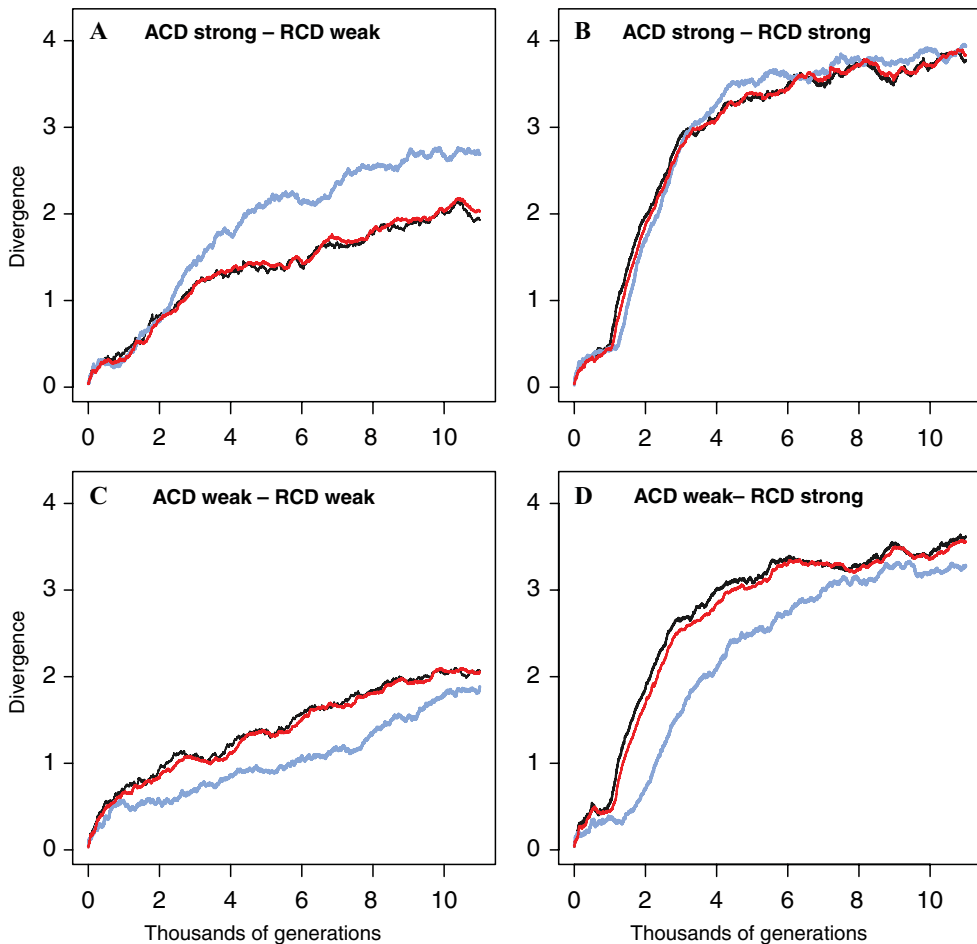
Figure 7. Simulation runs investigating RCD and ACD operating on the same trait from a model[151] based on the biology of *Hetaerina* damselflies (see the Case Studies section). Shown are the evolutionary trajectories of the species recognition cue (red line), the location parameter used for mate recognition (black line), and the location parameter used for competitor recognition (blue line). The strength of ACD was varied by changing the density of territories, and the strength of RCD was varied by changing the fecundity cost of heterospecific pairings. Either process alone can drive rapid divergence in the recognition cue in this model (not shown). Here, with both processes operating, divergence in the recognition cue closely tracks the central location of the female mate recognition function, whether selection against heterospecific pairings is weak (A, C) or strong (B, D). Male competitor recognition also diverges between the two species and can evolve faster than female mate recognition when ACD is strong and RCD is weak (A), but when RCD is strong, competitor recognition diverges because of selection on males to recognize conspecific competitors as the recognition cue diverges between species. Thus, in this model, sympatric shifts in competitor recognition can arise as a byproduct of RCD-driven divergence in the recognition cue.

in greater detail, on the problem of distinguishing ACD from RCD and ECD.

While the three character displacement processes are conceptually distinct, distinguishing among them empirically can be difficult. Evaluating which processes could be responsible for a sympatric trait shift requires a detailed understanding of how the trait functions—for example, how it affects social interactions—and how variation in the trait af-

fects fitness. Surprisingly few character displacement studies are this detailed.[4,98]

In cases of divergence in sympatry, it may not be possible to rule out any process a priori. For example, song divergence in sympatry could be caused by any one of the character displacement processes. Many bird and insect songs are used in the contexts of both mate recognition and competitor recognition.[99,100] Song playbacks to all classes of

potential heterospecific audiences (e.g., sympatric and allopatric males; sympatric and allopatric females) would be necessary to evaluate whether an observed shift in song could have been caused by RCD, ACD, or both processes. One might presume that sympatric shifts in song could not be driven by ECD, but shifts in song could potentially arise as a pleiotropic effect of shifts in morphological traits that affect resource use (e.g., beak size).[101] It cannot be assumed that shifts in traits that affect resource use are products of ECD. Any external trait that differs between species is a potential target of selection for improved species recognition. In theory, RCD could inadvertently reduce interspecific exploitative competition by causing divergence in body size,[102] and the same might be true for ACD.

Though it has been argued that shifts in mate recognition or competitor recognition can be taken as unambiguous evidence for RCD or ACD, respectively, this claim does not hold up to scrutiny. Selection arising purely from intraspecific interactions could cause the recognition functions of two species to diverge, if the trait upon which recognition is based was diverging for other reasons. However, showing that a trait is not used for mate recognition or competitor recognition would effectively rule out RCD or ACD, respectively. In the case of traits used for recognition in both contexts in sympatry, the state of allopatric populations may shed light on whether RCD or ACD played the leading role in divergence. Theoretical work on the relationship between RCD and ACD remains at an early stage, but a tentative conclusion is that RCD has priority over ACD if the same trait is used for recognition in both contexts (see Formal Theory). Thus, showing that mate choice and competitor recognition are based on the same traits in allopatric populations would weaken the ACD hypothesis. But finding that a displaced trait is used only for competitor recognition and not for mate choice in allopatric populations would suggest that ACD played the leading role in divergence.

If an interspecific interaction was strong enough in the past to cause divergence, it seems likely that the interaction would still occur at some detectable level in sympatry, but failing to detect it does not prove that the interaction was absent in the past. If allopatric populations are available, it may be possible to carry out experiments with the putative ancestral forms to estimate the strength of the interaction

at the time of secondary contact and compare it to the current interaction in sympatry. This approach has been used, for example, to test ECD predictions in sticklebacks in experimental ponds[98,103] and to test ACD and RCD predictions in damselflies in the field.[11,75,104,105]

Convergent ACD could not be confused with RCD or ECD in two-species systems, but in the case of multiple interacting species, divergence from one sympatric species could result in convergence on another.[106,107] Thus, focusing on single species pairs could yield false evidence for convergence. In the case of shifts in traits that are thought to affect interspecific fighting ability, it would be valuable (and novel) to determine whether such shifts actually affect fighting ability in the predicted direction.

ACD theory makes fairly specific assumptions about resource overlap. Divergent ACD does not require that the species have limiting resources in common. The only relevant resources are those to which interspecific aggression affects access. For example, whether species of rubyspot damselflies compete exploitatively for food at the larval stage has no bearing on whether it is beneficial for adult males to exclude heterospecific males from their territories. Simply showing that species overlap in resource use is not sufficient to support a hypothesis of convergent ACD. Convergent ACD should only be seen in cases in which interspecific aggression affects access to a common limiting resource. Quantitative estimates of the levels of intraspecific and interspecific resource competition, combined with model simulations, may be required to firmly establish whether selection would favor convergence or divergence in competitor recognition.

Accounting for plasticity

Responses to heterospecifics may often be developmentally plastic.[108] For example, damselfish (*Stegastes fasciolatus, Plectroglyphidodon lacrymatus*) can learn to recognize other species as competitors for food,[109–111] arrow cichlids (*Amphilophus zaliosus*) adjust their levels of aggression based on the breeding status of heterospecific competitors,[112] and great tits (*Parus major*) and blue tits (*P. caeruleus*) cross-fostered with heterospecifics learn to identify members of their foster-parent's species as territorial competitors.[113–115]

Developmentally plastic responses to heterospecifics could potentially result in the same

geographic patterns as ACD (e.g., enhanced discrimination in sympatry), without a genetic component to the geographic variation.[4] For example, some birds may be equipped with a learning mechanism that enables them to discriminate conspecific song from the song of novel heterospecifics.[116,117] Such birds might respond less aggressively to heterospecific song in the first generation after secondary contact than they would in allopatry, before selection in sympatry could possibly have any effect. Conversely, the capacity for social song learning may cause species to converge in song in sympatry, as appears to be the case for *Galerida* larks.[38] Responses to heterospecifics at the time of secondary contact are unlikely to be optimal, however, and thus selection in sympatry might be expected to favor alleles that modify the reaction norm. Evidence for such genetic changes would constitute evidence for ACD.[4] Conversely, unmodified reaction norms do not constitute evidence for character displacement processes, even if they are in the predicted direction.

In general, the process by which selection increases or decreases the relative influence of environmental cues in trait development is known as genetic accommodation.[118] To our knowledge, no study has explicitly tested for character displacement via genetic accommodation. This would require determining whether geographic variation in the reaction norm for a trait showing a character displacement pattern is heritable, for example, through reciprocal transplant, common garden, or cross-fostering experiments. The best example that we know of, though relating to RCD rather than ACD, addresses female mate recognition in *Calopteryx* damselflies.[105] Experiments investigating the effect of mating experience on species discrimination suggest that the learned response to *C. virgo* males of female *C. splendens* from allopatric populations is less pronounced than the same response of females from sympatric populations. If these differences in learning responses between allopatric and sympatric populations remained after reciprocal translocation experiments, this would constitute strong evidence that selection in sympatry favored individuals sensitive to environmental cues, leading to a heightened influence of learning (i.e., genetic accommodation). This view of character displacement, which places the focus on selection acting on the developmental machinery of trait production in relation to environmental inputs rather than simply

on the presumed genetic architecture coding for traits,[118] may lead to a deeper understanding of the ways that interspecific interactions drive adaptive evolution.[46]

Coexistence and species range limits

Most theoretical work on competition and species coexistence deals exclusively with exploitative competition or does not distinguish between exploitative and interference competition.[96] Models that explicitly incorporate interference competition show that it can change the predicted outcome and also that the specific form of interference matters for coexistence.[119,120] If two species are competing exploitatively for the same limiting resource, the superior resource exploiter is expected to drive the other species to extinction, unless they partition the resource in some way that reduces interspecific competition relative to intraspecific competition.[121] In the absence of resource partitioning, interspecific interference competition usually hastens competitive exclusion, although it can reverse the outcome.[120] If the inferior resource exploiter is superior in interference competition, then whichever species is initially most abundant is expected to prevail. The chief exceptions are forms of interference competition in which the inferior resource exploiter consumes or parasitizes the other species, which can lead to stable coexistence without resource partitioning.[120] On the basis of current theory, interspecific aggression is not the sort of interference competition mechanism that can promote coexistence in the absence of resource partitioning, unless specific conditions are met. Vance[122,123] showed that long-term coexistence is possible, without resource partitioning, if intraspecific interference is greater than interspecific interference for both species and this difference exceeds the advantage of the more efficient resource exploiter.

Evidence that intraspecific interference exceeds interspecific interference has been hypothesized to explain coexistence between species of *Plethodon* salamanders,[124] Interspecific competition in *Plethodon* appears to be mediated entirely by territorial aggression.[124–126] Whether the species would be in competition for limiting resources, such as food or refuges, in the absence of territorial aggression has not been established.[125] Thus, it is not clear that interspecific aggression promotes coexistence in *Plethodon,* but the finding that intraspecific

interference exceeds interspecific interference may indeed explain why these interference competitors are able to coexist. Interference competition has been hypothesized to stabilize coexistence between great tits (*Parus major*) and blue tits (*P. caeruleus*).[127] This hypothesis is based on evidence that great tits dominate blue tits in direct competition over nest boxes, which are limiting for reproduction,[127,128] while blue tits are superior in exploitative competition for food during the breeding season.[127,129] We have not found other putative cases of interspecific aggression promoting coexistence in the absence of resource partitioning, but this might merely reflect a lack of empirical research.

On the other hand, interspecific aggression may often be the primary mechanism through which animal species partition resources. In a particularly well-documented example, interspecific aggression is thought to enable two species of gerbils to coexist in the Western Negev Desert on the same food resource (seeds).[130,131] The smaller species, *Gerbillus allenbyi,* is subordinate in aggressive encounters but forages more efficiently at low seed densities than its congener, *G. pyramidum.* In allopatry, both species preferentially forage in the same habitat type in the early hours of the night, but in sympatry the subordinate species shifts to a different habitat type early in the night and forages later in the night in the preferred habitat. Field enclosure experiments demonstrated that the shift in habitat use by the smaller species is a direct response to the presence of the larger species.[132] This type of response to a dominant competitor is predicted by models of habitat selection based on optimal foraging theory.[133,134] In the absence of interference competition, the inferior resource exploiter, *G. pyramidum,* would be predicted to go extinct. Thus, the behavioral responses of both species to each other appear to be critical for their continued coexistence. Alternative mechanisms for coexistence based solely on exploitative competition have been tested and rejected for this system.[130,131]

How does interspecific aggression affect coexistence of species that are not competing exploitatively over common limiting resources? From an optimality perspective, interference mechanisms should not evolve in the first place unless the species are ecological competitors,[8,123] but this perspective overlooks the evolutionary history of interspecific aggression. In many cases, interspecific aggression has probably arisen as a byproduct of intraspecific aggression[8] and may be maintained at higher than optimal levels by genetic constraints or gene flow from allopatry. While interspecific aggression entails costs that should, in principle, reduce the carrying capacity of both species, the magnitude of the costs may be highly asymmetrical. When aggression involves defense of space (i.e., territoriality), aggression from a dominant species could prevent a subordinate species from gaining access to a limited resource, even if the resource is not used by the dominant species. The subordinate species might be able to avoid interspecific encounters through temporal or spatial shifts in habitat use,[10,34,132,135,136] but such behavioral shifts would further widen the cost differential by reducing the frequency of interspecific encounters. Thus, the two species might coexist in a suboptimal state, where the subordinate species pays the cost of avoiding interspecific aggression (e.g., by foraging in marginal habitat) and selection is too weak to eliminate heterospecific aggression in the dominant species (especially in the presence of gene flow from allopatric populations or a genetic correlation between conspecific and heterospecific aggression). The ecological and evolutionary dynamics are likely to be affected by the relative densities of the two species, however. If the subordinate species is present at higher initial density than the dominant species, then the net per capita cost of interspecific aggression could be higher for the dominant species even if the costs of individual encounters are higher for the subordinate species. We are not aware of any plausible scenario under which interspecific aggression would actually promote coexistence unless the species are also competing exploitatively.

Can interspecific aggression, alone or in combination with exploitative competition, determine species range limits? Price and Kirkpatrick[137] examined the conditions under which exploitative competition can generate evolutionarily stable range limits. In their model, two species initially specialize on different segments of the same resource distribution. In the absence of the competitor, each species is able to escape extinction and evolve into the other species' niche if the resource distribution shifts in that direction. In the presence of the competitor, the species that initially specialized on the declining segment of the resource distribution can be driven to extinction. If the resource shift occurs across space,

this process can result in evolutionarily stable species range limits. Price and Kirkpatrick[137] did not extend their model to include interference competition, but it seems likely that interspecific aggression would modify the predicted outcome. For example, if the species that is specialized on the declining resource is subordinate to the other species, then competitive exclusion would presumably occur at a higher level of the resource, resulting in a more restricted range for the subordinate species and a narrower zone of sympatry than expected in the absence of interspecific aggression. Conversely, if the species that is specialized on the declining resource is behaviorally dominant, it might be able to take over the niche of the subordinate species and drive it to extinction instead.

Interspecific aggression may explain some species range limits. In the case of two species of *Phylloscopus* warblers that are very similar in morphology and foraging behavior but differ in body size by 40%, the northern limit of the larger species coincides with a decline in the abundance of the large prey on which it specializes, but the southern limit of the smaller species does not coincide with a shift in the resource. [27,137,138] Gross and Price[27] inferred that the southern range of the smaller species is limited only by aggression from the larger species. As another example, eastern and western meadowlarks (*Sturnella* spp.) are largely allopatric but where their ranges overlap they can be found in close sympatry defending exclusive (nonoverlapping) territories. The two species are nearly indistinguishable in morphology and plumage but have distinctly different territorial songs and do not appear to interbreed (approximately 5% sequence divergence).[139] Neither species is clearly dominant over the other. Both respond aggressively to playbacks of the other species' territorial song in sympatry but not in allopatry.[140] Along their extensive contact zone in the Great Plains, both species have advanced into each other's range in some areas and retreated in other areas during the past century.[141,142] Given that these species compete directly for all-purpose territories, and that birds occupying different territories do not deplete each other's resources, interspecific exploitative competition must be minimal.[143] Thus, it seems likely that interspecific aggression is the mechanism most directly responsible for curbing post-Pleistocene range expansion of these ecologically equivalent species.

Species ranges can be especially narrow and sharply defined along elevation gradients. There are numerous examples of closely related species replacing each other in narrow transition zones. That these replacements are not just a result of adaptation to climatic factors and the associated fitness trade-offs is suggested by cases in which the elevation ranges of species contract in the presence of a likely competitor or expand where a competing species is absent.[144,145] Interspecific exploitative competition could account for such observations,[137,146] but the alternative hypothesis that interspecific aggression maintains the species boundaries is rarely tested. A logical first step toward testing the latter hypothesis is to determine whether species are aggressive to each other in the replacement zone. Jankowski *et al.*[147] used playbacks of territorial song to test for aggression between species of congeneric *Henicorhina* wood-wrens and *Catharus* thrushes both inside and outside of contact zones. Wood-wrens responded no differently to playback of heterospecific song than to conspecific song close to their contact zone, and less strongly to heterospecific song farther away from the contact zone. In *Catharus*, there were asymmetric responses in the contact zone with the low elevation species responding strongly to the high elevation species' song but not vice versa. Thus, while each species in a pair may be better adapted to a certain elevation range, interspecific aggression may be what actually maintains the range boundaries.[147]

Taking interspecific aggression into account may be necessary to accurately predict how changes in human land use practices and climate change will affect species ranges. For example, as the western bluebird (*Sialia mexicana*) has expanded its range northward, aggressive males on the leading edge of the expansion have taken over the territories of mountain bluebirds (*S. currucoides*), resulting in complete species replacement in some lower elevation areas in less than 10 years.[28] In this case, the dominant species is recolonizing parts of its natural range, as a result of nest box programs designed to replace nesting sites destroyed by logging, and the subordinate species is contracting back into its former range. In other cases, range expansion by behaviorally dominant species might make subordinate species vulnerable to extinction. For example, expanding cougar (*Puma concolor*) populations in western North America have been identified as a potential threat to lynx (*Lynx canadensis*)

populations.[25] In this and other cases of interference competition between carnivores, individuals of the larger species may actually kill individuals of the smaller species, with potentially devastating demographic consequences.[148,149]

Conclusions

The prevalence of interspecific aggression suggests that it should, by now, be quite well studied. It was indeed on the minds of ecologists in the 1970s, and some valuable contributions were made, but while research on other interspecific interactions exploded, interspecific aggression was largely ignored until quite recently. Much research remains to be done before interspecific aggression merits its own chapter in the textbooks. This is a wide-open field for both empiricists and theoreticians.

We have attempted to provide a useful review of recent progress in this area and some guidance for future research. We recommend that interspecific aggression be conceptualized and studied as a dynamic species interaction, not as a single-species optimization problem. Along with other mutually negative interactions between species, interspecific aggression should be recognized as an agent of character displacement. Naturally, researchers attempt to fit their data into existing theoretical frameworks, but expanding the established character displacement categories to encompass the effects of interspecific aggression is problematic. We recognize a third category, agonistic character displacement (ACD), which can roughly be defined as evolution caused by interspecific aggression (Fig. 1).

ACD can cause sympatric species to converge or diverge in the traits used for recognizing competitors, depending on whether aggression affects access to a common resource or only to species-specific resources (Figs. 2–6). ACD may also cause sympatric shifts in traits that affect interspecific encounter rates and fighting ability. Distinguishing divergent ACD from reproductive character displacement (RCD) empirically is difficult and may not be possible if the same traits are used for competitor recognition and mate recognition. Whether the same traits are indeed used for mate recognition and competitor recognition has rarely been investigated, and this is one of the key areas where empirical research is needed. Another empirical challenge is to distinguish evolutionary shifts from developmental plasticity, and this is a particularly salient issue for sympatric shifts in competitor recognition.

Theoretical work is needed to better understand the relationship between ACD and other evolutionary processes and to inform empirical studies. For example, a mathematical model based on territorial damselflies suggests that RCD has priority over ACD if mate recognition and competitor recognition are based on the same traits (Fig. 7), but the generality of this result remains to be established.

In theory, interspecific aggression can hasten competitive exclusion by reducing population growth rates or prevent competitive exclusion by counteracting an imbalance between species in the ability to exploit resources. Coexistence is favored by resource partitioning, and in some cases interspecific aggression may be the primary cause of resource partitioning. The extent to which interspecific aggression determines species range limits is currently unknown. It may be critical to take interspecific aggression into account to accurately predict the effects of climate change on species distributions.

The impact of interspecific aggression on species coexistence and range limits had not been reviewed previously and there is a general lack of continuity and little cross-referencing in this literature. We hope that this review stimulates further research in this area.

We have not attempted to review all of the ways that aggression between species might affect the course of evolution. For example, interspecific aggression may directly affect habitat selection in sympatry and alter one or both species' ecological niches,[37,133,136,150] with potentially cascading effects through the community.

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Conflicts of interest

The authors declare no conflicts of interest.

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